ADDITIONAL MATERIAL OF *DASYURUS DUNMALLI* FROM THE PLIOCENE CHINCHILLA LOCAL FAUNA OF QUEENSLAND AND ITS PHYLOGENETIC IMPLICATIONS

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New material of *Dasyurus dunmalli* from the Pliocene Chinchilla Local Fauna provides previously unknown data relevant to determining its phylogenetic position. The presence of a V-shaped lower incisor arcade in *D. dunmalli* detracts from the case for a special relationship between this fossil taxon and *Dasyurus maculatus*, suggested by a previous investigation. Parsimony-based analysis also supports a special relationship between *Sarcophilus harrisii* and *Dasyurus maculatus*. ❒ *Dasyuridae, Dasyurinae, Dasyurus dunmalli, Chinchilla Local Fauna, Pliocene, Queensland.*

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Determining the relationship of *D. dunmalli* to other *Dasyurus* has proven problematic with significant levels of homoplasy indicated regardless of phylogenetic interpretation (Bartholomai, 1971; Archer, 1982; Van Dyck, 1987; Wroe & Mackness, 1998). Hypotheses put forward to date include *D. dunmalli* as a sister taxon to: *D. viverrinus* (Bartholomai, 1971; Archer 1982); all extant *Dasyurus* (Archer, 1982); all extant *Dasyurus* except *D. hallucatus* (Archer, 1982); *D. spartacus* + *D. albopunctatus* (Van Dyck, 1987) and *D. maculatus* (Wroe & Mackness, 1998). Alternatively, Archer (1982) suggested that *D. dunmalli* may have shared no special relationship with any living species of *Dasyurus*.

A paucity of material has clearly constrained elucidation of the position of *D. dunmalli* relative to other *Dasyurus*. With the inclusion of newly discovered material from the Chinchilla Local Fauna we re-analyse the data and method presented by Wroe & Mackness (1998) in their parsimony-based investigation of relationships among species of *Dasyurus*.

Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar-premolar boundary, where the adult (unreduced) postcanine cheektooth formula of marsupials is P1-3 and M1-4. Dental terminology follows Wroe (1999). Systematic terminology incorporates amendments to Archer's (1982) classification as suggested by Krajewski et al. (1994) and Wroe (1996, 1997, 1999). QMF = Queensland Museum fossil collection.

SYSTEMATICS

DASYUROMORPHIA (Gill, 1872) Wroe 1996
DASYURIDAE Goldfuss, 1820
DASYURINAE (Goldfuss, 1820)
Krajewski et al., 1994

Dasyurus dunmalli Bartholomai, 1971
(Fig. 1)

REFERRED MATERIAL. QM F3357, partial right dentary, preserving roots of I_{1-3},C_1, P_1, and complete P_{2-3}, M_{1-2}.

LOCALITY AND AGE. North bank of the Condamine River, Chinchilla Rifle Range (26°48'S, 150°41'E). The Chinchilla Sand was named by Woods (1960) for a sequence of weakly consolidated grey to yellowish and light brown sands, ferruginised heterogeneous conglomerates, grits, sandy clay and clays. These outcrops range from shallow beds to sections several metres deep. The specimens described come from a fossil-bearing unit within the Wilkinson's Quarry that lies unconformably on an indurated layer of fine sand. The sediments are primarily fluviatile in nature and represent a number of depositional events. Most fossils in these units occur as isolated pieces. On the basis

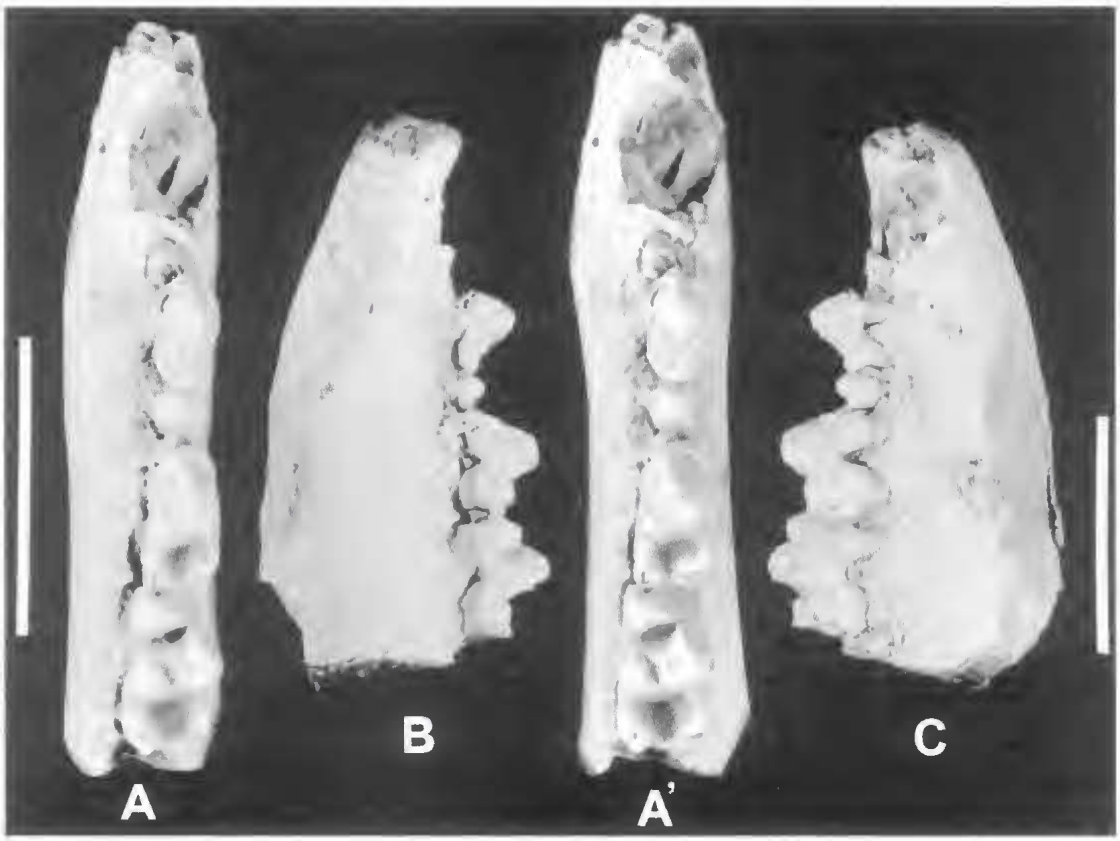

FIG. 1. *Dasyurus dunmalli*. QM F3357, partial right dentary, preserving roots of I_{1-3}, C_1, P_1, and complete P_{2-3}, M_{1-2} in A-A', stereo pair occlusal view; B, lingual view; C, buccal view. Scale bar = 1cm.

of biocorrelation with the Kanuka Local Fauna of the Tirari Desert in South Australia, Tedford et al. (1992) suggest an age of around 3.4 million years for the Chinchilla Local Fauna.

DESCRIPTION. The crowns of I_{1-3} are broken away. In anterior view, the root of I_1 is positioned ventral to that of I_2 and lingual to that of I_3. This gives a V-shaped lower incisor row. The anterior tip of the dentary is compressed on the lingual-buccal axis. Observable morphology of C_1, P_{1-3}, and M_{1-2} is consistent with that of other *D. dunmalli* from the Chinchilla Local Fauna, as described by Bartholomai (1971), Archer (1982) and Wroe & Mackness (1998).

PHYLOGENETIC ANALYSIS

The arrangement of the lower incisors and anterior of the dentary have not been previously described for *D. dunmalli*. This region differs between dasyurid taxa and is consequently of significance in phylogenetic reconstruction. In most dasyurids, the lower incisors form roughly a V-shaped profile in occlusal view. *Sarcophilus harrisii* and *Dasyurus maculatus*, with linear profiles, represent the only exceptions. Wroe & Mackness (1998) posited a special relationship between *D. maculatus* and *D. dunmalli* based on the results of a computer-generated parsimony analysis. We have re-run this analysis incorporating this additional character. In the process we detected some errors in both our own (Wroe & Mackness, 1998) character analysis, as well as that of Van Dyck (1987). Corrections and additions are listed below and have been added to Tables 1-2. Results are presented in Fig. 2. Dental measurements are given in Table 3. Method otherwise follows Wroe & Mackness (1998).

a) Wroe & Mackness (1998) and Van Dyck (1987) consider only two character states regarding the shape of the upper incisor row (V-shaped and U-shaped). As observed by Archer (1976), a third state is evident in *D. maculatus* and *Sarcophilus harrisii*, i.e. 'straight'.

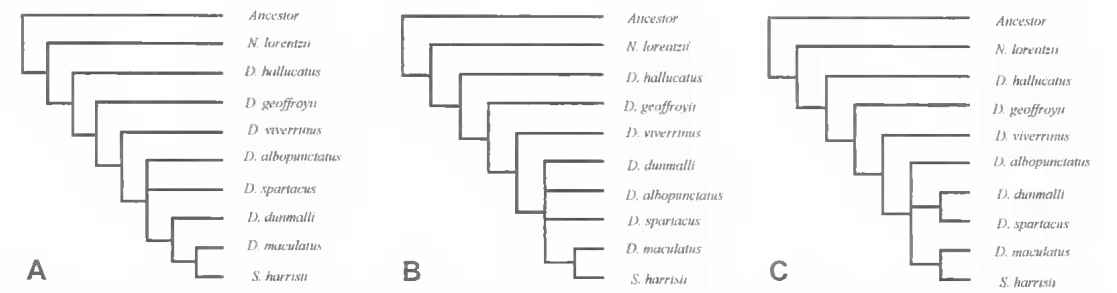

FIG. 2. Three most parsimonious trees (A, B, C) of 39 steps produced using PAUP 3.1.1 for seven species of *Dasyurus*, *Neophascogale lorentzii* and *Sarcophilus harrisii*. Analysis used DELTRAN optimisation and the branch and bound search option. Strict majority-rule consensus produced a tree identical to tree C.

b) Wroe & Mackness (1998) and Van Dyck (1987) score *Dasyurus hallucatus* as showing plesiomorphic phallic morphology. However, Archer (1974) and Woolley & Webb (1977) note that an erectile organ is present in *D. hallucatus*. Indeed, Archer (1974) describes it as identical to that of *D. geoffroii*.

c) Historically, a number of morphologists have argued for the recognition of possible monophyly for *D. maculatus* and *Sarcophilus harrisii* (see Ride, 1964; Archer, 1982). Some, but not all, recent molecular-based studies have supported this contention (Krajewski et al., 1994, 1997). Also, some molecular investigations have suggested that phascolosoricines (sensu Archer, 1982) represent the sister clade to *Dasyurus* and *Sarcophilus*. Consequently, we have included both *S. harrisii* and *Neophascogale lorentzii* in the re-analysis of data presented by Wroe & Mackness (1998).

d) Characters 12 and 17 in the analysis by Wroe & Mackness (1998) are unambiguously correlated. Consequently, we have removed character 12. Re-running the analysis produced 3 most parsimonious trees of 39 steps with uninformative characters excluded: CI = 0.806, HI = 0.194, RI = 0.875 and RC = 0.718 (Fig. 3). In all 3 trees, *D. dunmalli* formed a monophyletic clade with *D. albopunctatus*, *D. spartacus*, *D. maculatus* and *Sarcophilus harrisii*. This group was united by the following synapomorphies: premolars large, ovate in occlusal view (C 5); hypertrophy of M2 trigonid relative to talonid (C 14); and intermediate reduction of the metaconid (C 15). In one of these trees (C), a special relationship was evident between *D. dunmalli* and *D. spartacus*. In another (A), *D. dunmalli* appeared as the sister taxon to *D. maculatus* + *Sarcophilus harrisii*. Curiously, in neither case was the monophyly of *Dasyurus dunmalli* with either of these clades supported by any

TABLE 1. Characters and character states used in phylogenetic analysis with '*0*' = plesiomorphic, '*1*' = apomorphic and '?' = missing.

1. Diastema between $I^{1\text{-}2}$. *0*, present; *1*, absent.
2. I^1 morphology. *0*, hypsodont relative to I^2; *1*, not hypsodont relative to I^2.
3. Shape of incisor row. *0*, V-shaped; *1*, U-shaped; *2*, straight.
4. C_1 morphology. *0*, proportionate to uppers. *1* not proportionate.
5. Premolar morphology. *0*, premolars narrow and small in occlusal view; *1*, large and ovate in occlusal view.
6. Premolar occlusion (ordered). *0*, shear past each other in occlusion; *1*, do not shear past one another in occlusion.
7. P_3 retained/lost. *0*, retained; *1*, lost.
8. M_3 postmetacrista/paracristid length (ordered). *0*, shorter than in M_2; *1*, about equal to M_2; *2*, clearly longer than in M_2.
9. Position of metacone relative to stylar cusp D on M^1. *0*, perpendicular relative to st D; *1*, not perpendicular (i.e., posterobuccal).
10. Paracone morphology (ordered). *0*, unreduced; *1*, intermediate; *2*, greatly reduced.
11. Distance between metacone and stylar cusp B (ordered). *0*, not approximated; *1*, intermediate; *2*, approximated.
12. Molar shape. *0*, not bulbous; *1*, bulbous.
13. Posterior cingulid. *0*, well developed; *1*, reduced or lost.
14. M_2 trigonid vs talonid length. *0*, trigonid equal to or less than talonid in length; *1*, trigonid > in length than talonid.
15. Metaconid size (ordered). *0*, unreduced; *1*, intermediate; *2*, greatly reduced.
16. M_4 morphology. *0*, entoconid present; *1*, entoconid absent.
17. Skull height. *0*, low; *1*, high.
18. Rostrum beneath lachrymals. *0*, not broad; *1*, broad.
19. Penis morphology. *0*, simple; *1*, complex.
20. Hallux morphology (ordered). *0*, present; *1*, reduced; *2*, absent.
21. Hind foot morphology. *0*, pes short and broad; *1*, elongate.
22. Lower incisor row. *0*, V-shaped; *1*, straight.

TABLE 2. Taxon/character matrix based on the distribution of 22 characters using the 7 species of *Dasyurus*, as well as *Neophascogale lorentzii* and *Sarcophilus harrisii*. Modified from Wroe & Mackness (1998).

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neophascogale lorentzii	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dasyurus hallucatus	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0
Dasyurus viverrinus	1	1	1	1	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0
Dasyurus dunmalli	?	?	?	1	1	?	0	?	?	?	?	0	0	1	2	?	?	?	?	?	?	0
Dasyurus albopunctatus	1	1	1	1	1	2	1	2	1	2	1	0	1	1	2	1	0	0	1	1	0	0
Dasyurus spartacus	1	1	1	1	1	2	1	2	1	2	1	0	1	1	2	1	1	1	1	1	0	0
Dasyurus geoffroii	0	0	1	1	0	2	1	1	1	2	1	0	1	0	1	0	1	1	0	0	0	0
Dasyurus maculatus	1	1	2	1	1	2	1	3	1	2	2	1	0	1	3	0	0	0	1	1	0	1
Sarcophilus harrisii	1	1	2	1	1	2	1	3	1	2	2	1	1	1	3	0	0	0	1	1	0	1

synapomorphy. A third tree (B) also treated *D. dunmalli*, *D. spartacus*, *D. albopunctatus*, *D. maculatus* and *Sarcophilus harrisii* as monophyletic, but within this clade, only the position of *S. harrisii* and *Dasyurus maculatus* as sister taxa was resolved. A strict majority-rule consensus produced a phylogeny identical to this third tree. In all trees, a special relationship between *Sarcophilus harrisii* and *Dasyurus maculatus* was supported by the following synapomorphies: development of a straight upper incisor row (C3); marked elongation of the M3 postmetacrista/paracristid relative to that of M2 (C8); approximation of stylar cusp D and the metacone (C11); development of bulbous molars (C12); development of greatly reduced metaconids (C15) and the development of a linear lower incisor row (C22).

In our view, these results provide no support for the existence of a special relationship between *D. maculatus* and *D. dunmalli* as postulated by Wroe & Mackness (1998). Moreover, although on the face of it, the results of this analysis seemingly provide equivocal support for the monophyly of either *D. dunmalli* + *D. spartacus* or *D. dunmalli* + *D. maculatus* + *Sarcophilus harrisii*, the absence of potential synapomorphies uniting either clade provides no real foundation on which to base these phylogenies. Consequently, we consider the position of *D. dunmalli* unresolved within a clade inclusive of *D. albopunctatus*, *D. spartacus*, *D. maculatus* and *Sarcophilus harrisii*. In this regard, both the present study and those of Van Dyck (1987) and Wroe & Mackness (1998) largely concur, excepting the placement of *S. harrisii*, which was not included in the latter two studies. Support for the monophyly of *S. harrisii* and *Dasyurus maculatus* will require further testing using an expanded taxon/character matrix for corroboration.

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TABLE 3. Dental measurements (mm) of QM F3357. l = anteroposterior length; w = maximum width (premolars); w1 = maximum transverse dimension of trigonid; w2 = maximum transverse dimension of talonid.

Taxon	QMF No.	P_2		P_3		M_1			M_2		
		l	w	l	w	l	w1	w2	l	w1	w2
D. dunmalli	3357	4.3	2.4		2.0	1.8	5.4	2.7	3.1		6.7

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